Biol. Rev. (1983), **58**, *pp.* 485–520
Printed in Great Britain

MATING SYSTEM AND SEXUAL DIMORPHISM IN LARGE, TERRESTRIAL, MAMMALIAN HERBIVORES

BY PETER JARMAN

Department of Ecosystem Management, University of New England, Armidale, N.S.W. 2351, *Australia*

(*Received* 19 *November* 1982, *accepted* 6 *January* 1983)

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I. INTRODUCTION

Darwin (1871), exploring the relationships between mating systems and sexual dimorphism, drew most of his examples and arguments from birds; these have continued to contribute heavily to studies of mating systems and strategies, and to theories about sexual dimorphism. While their numbers and observability make birds ideal animals from which to draw broad truths about behavioural ecology, they illustrate complexities of social organization poorly. Most relevantly here, few bird species approach the degrees of dimorphism, or the complex forms of intrasexual competition, found in large, terrestrial, herbivorous mammals; some grouse Tetraonidae, bustards Otididae, and pheasants Phasianidae are exceptions to this.

In a sexually dimorphic species adult males and females differ consistently in size, colouring, shape or adornment, discounting primary differences in genitalia. Dimorphism might also imply differences in smell, calls and aspects of behaviour, but is not used in those senses in this paper. (However, dimorphism is used, as in the paper's title, to mean the general subject of physical similarity or dissimilarity between the sexes.)

Darwin (1871) argued that components of sexual dimorphism were selected because they bestowed advantages on their possessors in intrasexual competition for mates. Other components, he realized, were adaptations to sexual differences in raising young. These latter were moulded by 'natural' selection, the former by 'sexual' selection, which might or might not involve a female choosing between suitors. After a century of discussion, these ideas were brought up to date by contributors to *Sexual Selection and the Descent of Man 1871–1971* (Campbell, 1972).

The general association between mating systems and sexual dimorphism in birds has often been noted (Lack, 1968; Orians, 1969). Selander (1972, p. 210) said: "in many [bird] groups the correlation between mating systems and degree of sexual dimorphism ... is so strong that the mating type can be inferred with reasonable certainty from the degree of dimorphism". He pointed out that size monomorphism is generally associated with monogamy, while males are often larger than females in polygynous or poly-brachygynous species. Trivers (1972) held that relative parental investment of the sexes correlates most closely with sexual selection. The sex investing less in its offspring must compete for mates and will thus be subject to sexual selection upon those heritable traits that affect an individual's relative reproductive success. Emlen & Oring (1977) further argued that enviromental factors limit the extent to which the lesser-investing sex can control access to the other. The more that members of one sex can monopolize access to the other, the greater is the likelihood of polygamy arising. The form of mating system and intensity of intrasexual selection in the lesser-investing sex are therefore determined by the environment and the most individually profitable means of monopolizing access to the other sex. If sexual dimorphism is indeed a product of sexual selection, then dimorphism should also reflect the combined influences of environmental factors and means of monopolization.

Ralls (1977) found that the bird-derived generalizations of Verner & Willson (1966), Orians (1969), and Selander (1972) applied poorly to mammals, despite their having been applied to all vertebrates by Brown (1975) and Wilson (1975). In an analysis of the relationships between male parental investment, mating system, and degree of dimorphism in all mammals she found that although large parental investment by males is a good predictor of monogamy, small parental investment by males is a poor predictor of extreme polygyny; monogamy is a very good predictor of both large parental investment by males and little sexual dimorphism; extreme polygyny is a good predictor of small parental investment by males and a very good predictor of extreme sexual dimorphism; little sexual dimorphism is a very good predictor of monogamy but a poor predictor of large parental investment by males; and extreme sexual dimorphism is a very good predictor of extreme polygyny and a good predictor of small parental investment by males.

For this paper, the important points in Ralls's analysis are that most strongly dimorphic species are strongly polygynous and vice versa, and their males usually invest little in offspring, but that many mammal males invest very little in offspring without the species being either extremely polygynous or extremely dimorphic. Ralls inferred that lack of parental investment by males is not enough by itself to explain extreme polygyny and dimorphism in mammals. She cited Wiley's (1974) suggestion that bimaturism (distinct differences between males and females in age at sexual maturity) is an important corequisite, with low male parental investment and an appropriate resource environment, in the evolution of extreme polygyny and dimorphism. Wiley argued that bimaturism would arise only where postponed reproductive effort by males increased their early survival or where male fecundity increased with age.

In summary, the current arguments for the evolution of dimorphism in mammals are: (i), that extreme dimorphism arises through competition between males for the opportunity to mate with females (which are usually the greater-investing sex in mammals); (ii), that strong competition occurs if some males have the opportunity to monopolize matings by limiting the access by other males to females; (iii), that environmental factors, mainly the dispersion and forms of resources, will (largely through their effects upon the dispersion and mobility of, and timing of reproduction by, females) determine whether, and in what way, some males can limit the access of others to females for mating; and (iv), that delayed maturation of males relative to females is necessary for the evolution of extreme polygyny and dimorphism.

Ralls (1977) also pointed to a general association between the occurrences of bimaturism, polygamy, high dimorphism, and large body size. Jarman (1974) associated the degree of sexual dimorphism in antelopes with body size, feeding style, grouping and social organization in the populations. These studies, and others, while not contradicting the general explanations for the evolution of dimorphism given above, suggest that those explanations are incomplete in details. There is considerable variation in the degree or form of expression of dimorphism amongst mammals, which remains to be explained. This paper explores that variation in three families of large terrestrial, herbivorous mammals (Bovidae, Cervidae and Macropodidae), analysing associations between body size, and dimorphism in weight, appearance and weaponry. It emphasizes the importance of considering the form of growth when describing dimorphism. It categorizes dimorphism amongst these mammals, and argues the adaptiveness of the types of dimorphism in terms of the mating strategies pursued by males. In doing so it strongly suggests that polygyny, like monogamy (Kleiman, 1980), is a phenomenon arising from diverse causes, which need clearer separation and definition in sociobiological discussion.

II. HYPOTHETICAL BASE

Wiley's (1974) derivation of bimaturism can be extended. In a population of an iteroparous species of mammal, each sex will be selected to survive for more than one breeding season, although not at the cost of reproducing. Females should select a mate possessing an inheritable tendency to survive; this will lead to selection for signals of survival in males. Prolongation of body growth, or, more cheaply, weapon growth, would provide simple signals, and would enable older, larger and better-armed males to suppress the reproductive efforts of younger males, if the socio-ecological context permits. Males that eventually breed will be those that, as young males, adopted strategies of survival rather than competing dangerously for matings against the older males. Bimaturism will arise.

Such differentiation in body size, weaponry and behaviour between age classes of sexually mature males will accentuate selection for well-signalled male survival. Under such selection, the optimum, signalled age, for males competing to breed, will rise until a further rise would secure that age class no greater proportion of the population's matings. This limit will be set either by the breeding males' inability to meet the cost of denying access to females to the increasing proportion of younger males in the population, or by the typical dispersion of females and the males' own ranging abilities. These last arise from the characteristics of the species' size, habitat, food and anti-predator behaviour (Jarman, 1974; Jarman & Jarman, 1979).

Underlying assumptions in this paper are: (i), that females mate so as to maximize their production of surviving offspring (hence a mating system based upon males using force upon females is most unlikely to be evolutionarily stable) and to link their genes with those most likely to disperse in the population. Thus the greater the differentiation amongst males in reproductive success, the stronger will be selection upon females for behaviour leading to optimal matings; (ii), that when an individual or class of males prevents others from associating with oestrous females, a female has nothing to gain by choosing a mate from outside that individual or class; but that, when mating occurs in a context of general association between sex- and age-classes, behaviour by the oestrous female differentiating among the males (as well as inter-male behaviour) may be necessary to guarantee her the most profitable mating. In such circumstances signalling of male status to both males and females could be important.

These arguments predict: that dimorphism will characterize species in which some males monopolize matings; that prolonged male growth in size of body and weapons will restrict this monopolization to certain age-classes of males; and that dispersion of females relative to the males' range will limit the extent of dimorphism and affect the age at which males first breed.

III. FAMILIES AND DATA CONSIDERED

The following reviews of forms of dimorphism and mating systems consider mainly three extant, recently radiated families of large, terrestrial, mammalian herbivores: Bovidae, antelopes, cattle, sheep, goats, etc.; Cervidae, deer; and Macropodidae, kangaroos, wallabies and rat-kangaroos. The first two are eutherian and all but their smaller species typically carry cranial weapons in at least the males; the third is metatherian and its species have neither cranial weapons nor tusks. Those traits apart, the three families are ecologically and behaviourally broadly comparable, although no extant macropodids are as large as, and therefore ecologically comparable to, large bovids and cervids Each family displays a range of forms of species-typical social organization.

These families are reviewed because of their comparability (allowing a search for evolutionary parallels between families), and because the necessary data are available for a representative array of their species. The analyses required data on growth, adult weight or height for both sexes, appearance, size of horns or antlers, and details of mating systems and ecology. Two other major radiations of herbivorous mammals, primates and rodents, have not been considered here because their climbing, burrowing and tree-dwelling make them in several ways incomparable with the families considered. Some comments are made, however, on some of the less numerous families of large, terrestrial, mammalian herbivores.

Species are referred to by colloquial names, scientific names being listed in Appendix 1. Sources of data, other than my unpublished studies, appear in Appendix 2.

In the analyses, weaponry refers only to horns or antlers; canine teeth or feet, which may be used offensively, are ignored. Dimorphism in appearance has been judged subjectively by the ease with which I could distinguish the sexes visually without considering weapons. It summarizes the ability of the animals' colouring, adornments and shapes (including fighting-related musculature in some species) to signal their sexes visually and at a distance. Weapons, while primarily offensive and defensive in function, may of course also have a secondarily signalling role. The distinction between weaponry and appearance has been made because they have evolved under different selective pressures.

(1) *Dimorphism and growth in Bovidae*

The range of habitats, foods, ecological strategies, social systems, and sizes of the 107 extant species of Bovidae (Simpson, 1945) makes this family a good subject for a study of dimorphism. Males of all species have horns, with which they fight in a variety of ways. Some develop shock-absorbent bone bosses to the horns, or dermal shields which prevent wounds from horn-tips. These structures may not develop fully in males until long after physiological sexual maturity; they are usually less well developed in females. In some species females also bear horns, which are used commonly in undamaging intrasexual aggression, occasionally in defence of young, and rarely in intersexual fighting. Adult males of a few species develop colours that distinguish them from females and young males. Males of many more species develop manes, crests, dewlaps, and other structures, which exaggerate the head, neck or shoulders seen frontally or in profile. In males of many species, the muscles of the neck and pectoral girdle are considerably larger than in females or young males. Adult males of most species are larger in linear measurements and weight than are adult females, despite equality or only slightly larger male size at birth (K. Ralls, pers. comm.). However, in a quarter of the species, small bovids in the Cephalophinae, Neotraginae and Madoquinae, listed by Ralls (1976), adult females are on average heavier or longer than males.

Analyses of the available data for species of Bovidae show that the possession of weapons does not correlate with similarity in appearance of the sexes (Fig. 1). Adult males resemble females in colouring and adornments, as often in species in which only males bear horns as in species in which both sexes are armed. However, there is a strong tendency for males that are much heavier than females to differ from them in appearance, and for the sexes to look alike in species in which their weights approach parity. There is no such relationship between possession of weapons by, and difference in weights between, the sexes.

With male weight to indicate species size (too few female weights are available), great differences between the sexes in appearance are found to characterize medium to very large species, mainly over 80 kg (Fig. 2), a point made by Walther (1966). The sexes of small species, under 20 kg, look alike. However, the sexes of many medium to large species also look alike. Among species whose sexes differ in appearance, the largest differ because the male's shape is exaggeratedly different from females, while in medium-sized species the sexes differ in colouring. Male weight less clearly predicts the possession of weapons by the sexes (Fig. 3). Females of very small species tend not to have horns, while both sexes have horns in species whose males weigh over 300 kg. So differences between the sexes in appearance and the possession of horns are predictable only at the extremes of the size range in extant bovids; in mid-range these aspects of dimorphism are unpredictable and vary independently.

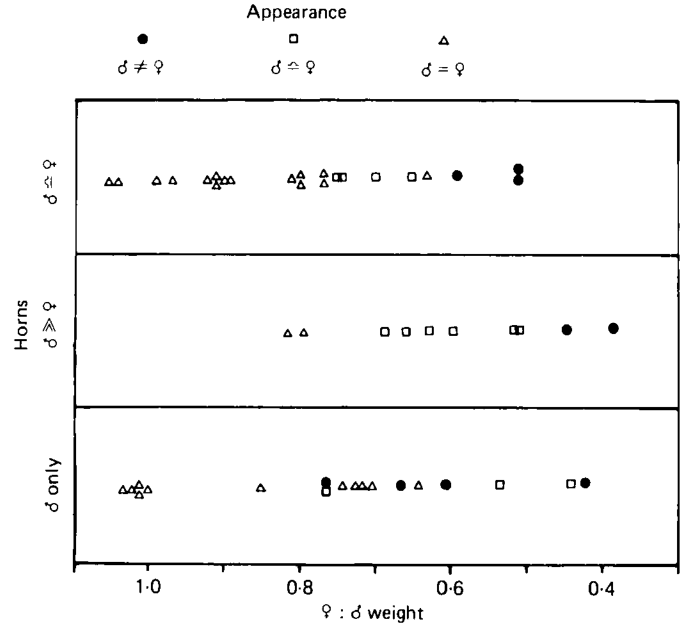

Fig. 1. Relationships, in 50 species of Bovidae, between the similarity of the sexes in weight, appearance (other than horns), and the possession of horns. Species are categorized as having sexes that are dissimilar (black spots), fairly similar (open squares), or closely similar (open triangles) in appearance; and possessing horns in males only, or in both sexes but much smaller in females, or which are similar in males and females.

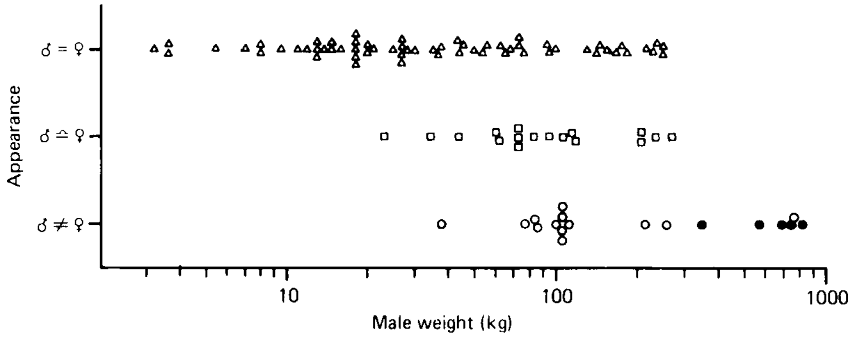

Fig. 2 Relationship, in 97 species of Bovidae, between the average weight of adult male and similarity between the sexes in appearance (other than horns). Species are categorized as having sexes that are closely similar (triangles), fairly similar (squares), or dissimilar (circles and black spots), in appearance. Black spots indicate that difference depends mainly on body shape; circles, that it depends on colouring and adornments.

Differences between the sexes in body weight are most extreme in the middle of the bovid size range (Fig. 4). Females weight 65 % or less of male weight only in species whose males weigh between 30 and 150 kg, and in the heavier nilgai, gaur, and some populations of American bison. No females in that weight-range exceed 80 % of male weight, except for serow and three large duiker species. There is a similar mid-range peak in male relative horn-size against body weight (Fig. 5). Males between 30 and

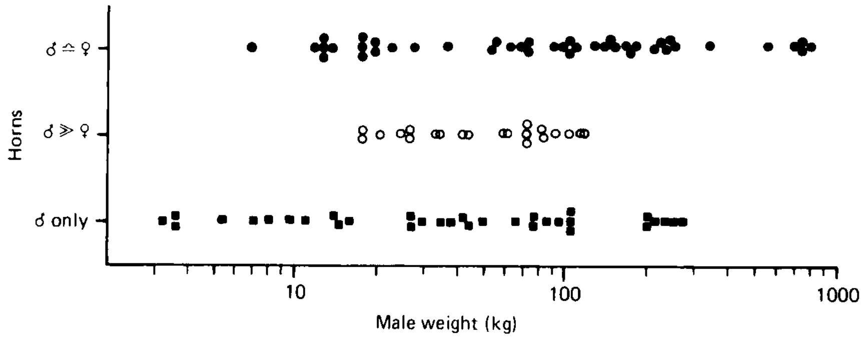

Fig. 3. Relationship, in 97 species of Bovidae, between the average weight of an adult male, and possession of horns by the sexes. Possession of horns is categorized as in Fig. 1.

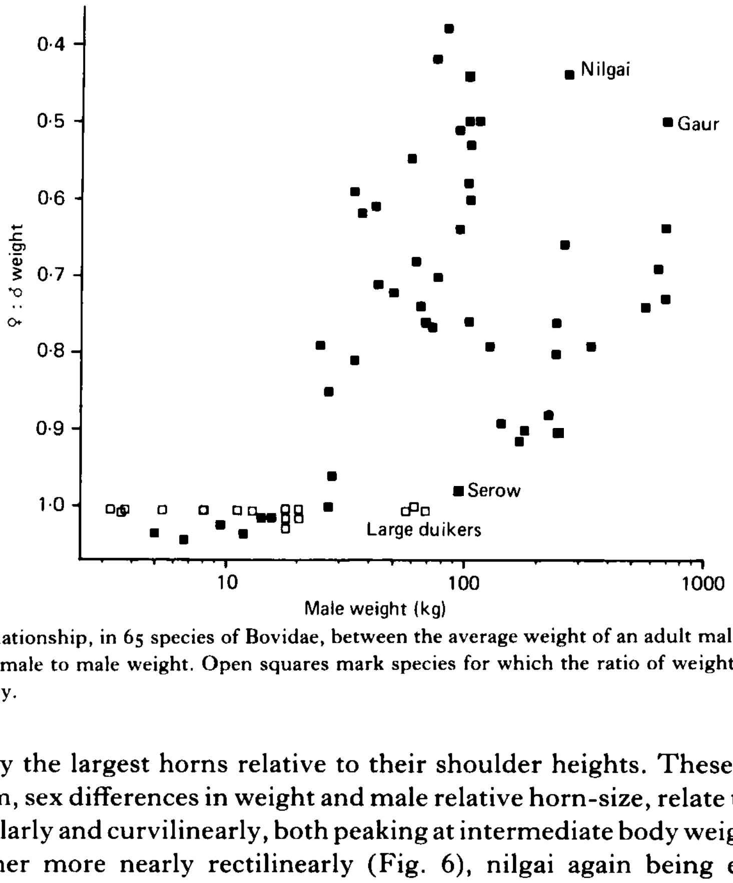

Fig. 4. Relationship, in 65 species of Bovidae, between the average weight of an adult male, and the ratio of adult female to male weight. Open squares mark species for which the ratio of weights was assumed to be parity.

300 kg carry the largest horns relative to their shoulder heights. These two aspects of dimorphism, sex differences in weight and male relative horn-size, relate to specific body weight similarly and curvilinearly, both peaking at intermediate body weight. They relate to each other more nearly rectilinearly (Fig. 6), nilgai again being exceptional. In Bovidae, relative male horn length is a good predictor of sexual dimorphism in size, and *vice versa*, although predictability is poorest in the mid-range.

Among the Bovidae there are three forms of growth to maturity. In the first, represented by small duikers and dik-diks (Kellas, 1955; Dittrich, 1967; Dittrich & Boer, 1980; Hutchinson, 1970), males and females reach an adult weight simultaneously early in life and remain at about that weight thereafter. In the second, females grow

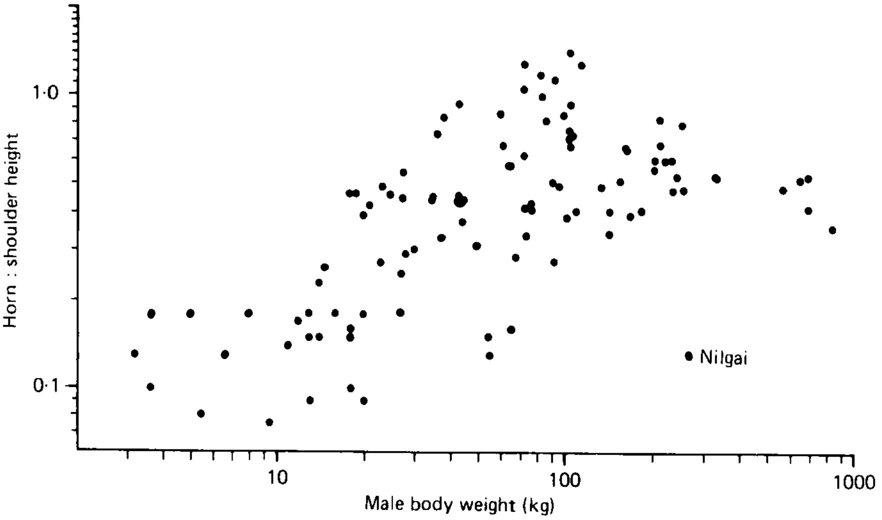

Fig. 5. Relationship, in 99 species of Bovidae, between the average weight of an adult male, and ratio of male horn length to shoulder height.

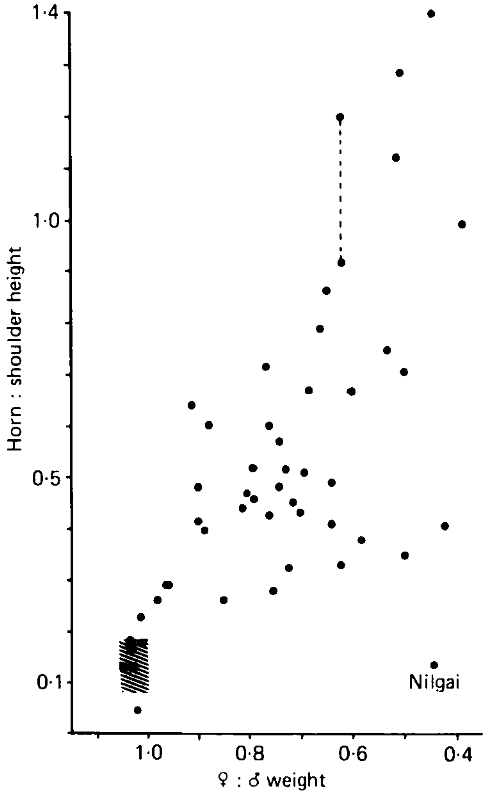

Fig. 6. Relationship, in 60 species of Bovidae, between the ratio of adult female to male weight, and the ratio of male horn length to shoulder height. The shaded area contains datum points for an additional 12 Cephalophinae, three Madoquinae, and four Neotraginae. The vertical broken line indicates the range of values of relative horn length recorded for races of *Ovis orientalis*, urial and mouflon.

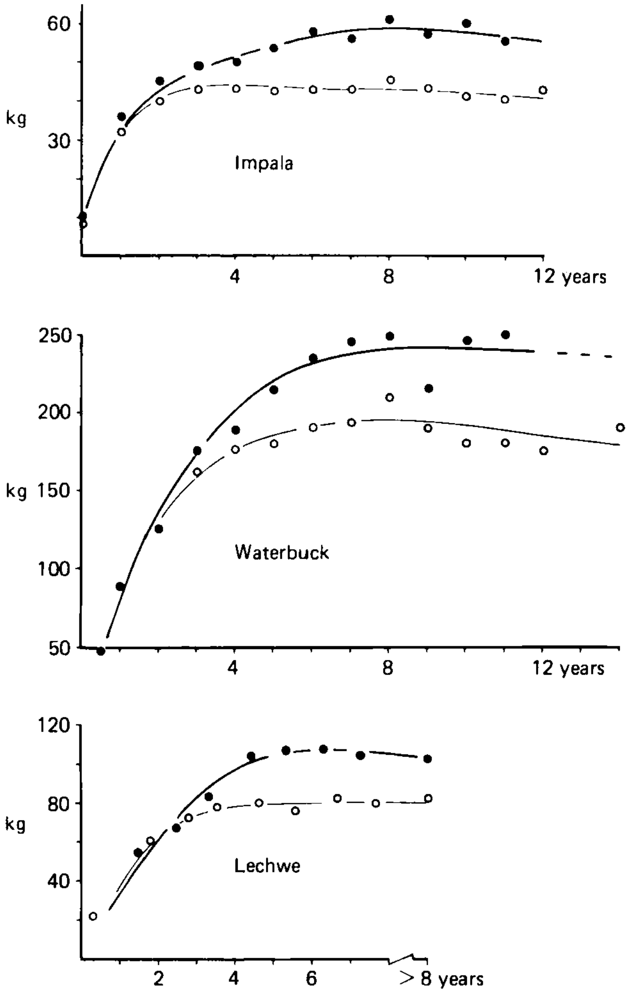

Fig. 7. Growth curves for impala, waterbuck and lechwe. Upper curves (black spots) in each are values for males, lower curves (open circles) for females. Data from Howells & Hanks (1975), Spinage (1969), and Robinette & Child (1964). Curves fitted by eye.

quite quickly to a steady, mature weight; males grow faster and for longer, reaching mature weight one to several years after females. They then maintain that weight (allowing for seasonal fluctuations) until old-age or death. Examples of this form are impala, waterbuck and lechwe (Fig. 7). Bighorn rams grow for 8 years before increase in skull weight ceases, while ewes do not increase in body weight beyond 4 years (Blood *et al.*, 1970). Dall sheep are similar (Bunnell & Olsen, 1976).

In the third form, males grow almost throughout life, sometimes declining in weight in old age; females may or may not do the same, but their growth rate is always less than that of males. This form is exemplified by the African buffalo (Fig. 8), the American bison (D. Lott, *in litt.* to Ralls, 1977), and probably musk ox.

The second and third forms lead to differences in size between adult males and females. The forms may intergrade, but their clearest examples are associated with

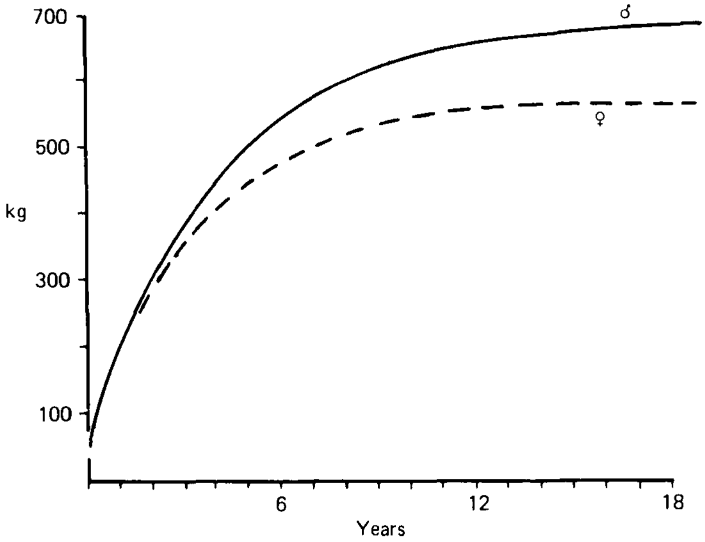

Fig. 8. Growth curves for male and female African buffalo. Data from Sinclair (1977).

different male strategies of aquiring mates. The second form matches Wiley's (1974) 'bimaturism', but the third does not. The terms ***determinate bimaturism*** for the second form, and ***indeterminate bimaturism*** for the third might emphasize the difference.

(2) *Dimorphism and growth in Cervidae*

There are over fifty species of deer, ranging in size from 9 to 800 kg. Males of all except two genera develop antlers, which are carried by females only in caribou (reindeer). Like the smallest bovids, the smallest deer species have rounded backs, short legs, cryptic colouring and inconspicuous weapons. Canines, longer in males than females, are the sole weapons in musk and Chinese water deer. Tufted deer males have minute antlers hidden in tufts of hair. Both sexes of muntjac have pedicles, which bear simple, short antlers in males and bony knobs in females. The antlers of pudus and brocket deer are short simple spikes. All these species grow canines in both sexes, and males and females are closely similar in colouring, shape and weight, which ranges from 9 to 20 kg.

Males of medium and large species of deer carry, when mature, larger and more complex antlers. Males of Andean deer of huemuls, weighing about 50 kg, carry simple, two-tined, short antlers; both sexes have canine tusks, but these do not project beyond the lip as in musk or Chinese water deer. Roe buck, at 20–30 kg, usually have one or two short tines on short antlers. Swamp deer, weighing up to 100 kg, carry four-tined, prominent antlers. In the genera *Odocoileus*, *Axis*, *Dama*, *Cervus*, *Rangifer* and *Alces* proliferation of tines or palmate development on antlers accompanies increasing male size.

However, the relative size of the antlers, expressed as antler-length relative to shoulder-height, is greatest in the mid-range of body-sizes of deer species (Fig. 9); this can be compared with a similar distribution of horn-sizes in bovids (Fig. 5). This finding may be compared with the analyses of Gould (1974) and Clutton-Brock *et al.* (1980), who found simple allometric relationships between antler-length and shoulder-height

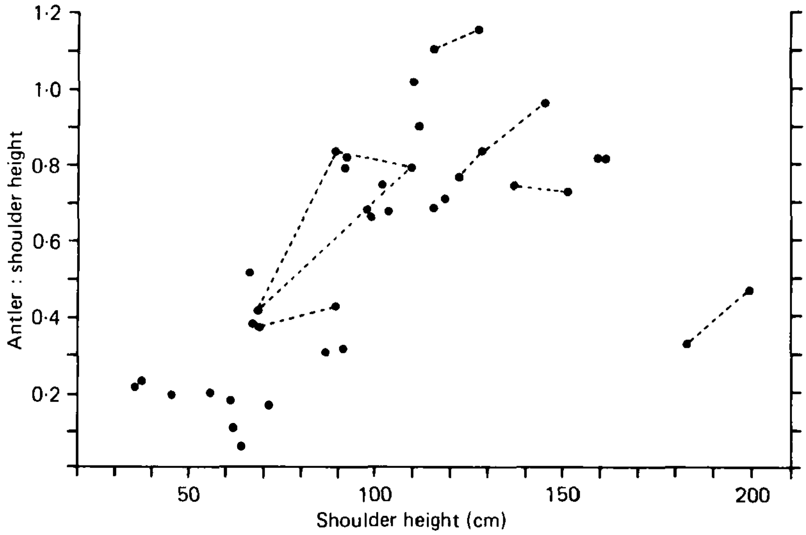

Fig. 9. Relationship, in 30 species of Cervidae, between the relative size of antler (expressed as the ratio of antler length to shoulder height) and shoulder height of males. Races of species are joined by broken lines.

in deer. Nevertheless, their data and mine show that moose bulls carry relatively short antlers for their body-size, and that the greatest relative lengths are found in the smaller caribou.

Antlers, unlike bovid horns, are deciduous and can regrow in new shapes. The number of tines of medium- and large-bodied deer increases with each new set of antlers for some years after sexual maturity. The maximum number of tines varies between individuals, and between geographical races which differ much in body-size, in several species. The typical number of tines on a mature head is difficult to determine, especially since data are biased towards trophy heads with exceptional numbers of tines. Nevertheless, an analysis comparing conservative estimates of mean maximum number of tines with male shoulder height (Fig. 10) shows number of tines increasing steadily with body size, although some large species such as wapiti and sambar have relatively simple antlers for their size and the medium-sized Schomburgk deer, relatively complex. Species with palmated antlers, fallow deer, moose and caribou (partially palmate), have disproportionately many tines, but most of these are short and not visually prominent.

Complexity of antlers expressed as the number of tines per length of antlers (Fig. 11) shows large species to have antlers that are less branched per unit absolute length. However, complexity expressed as the number of tines per length of antler relative to shoulder height (Fig. 12) suggests no significant trend in complexity with body size. This suggests that complexity of antler branching relative to length has a function that is constant with specific body size, such as mechanical properties of offence and defence, while relative antler length, peaking in the middle of the range of species' body-sizes, appears to have a function that changes with body-size.

Dimorphism in appearance other than weaponry seems to be confined to deer species over about 40 kg. It takes the form of development of a thickened neck and structures,

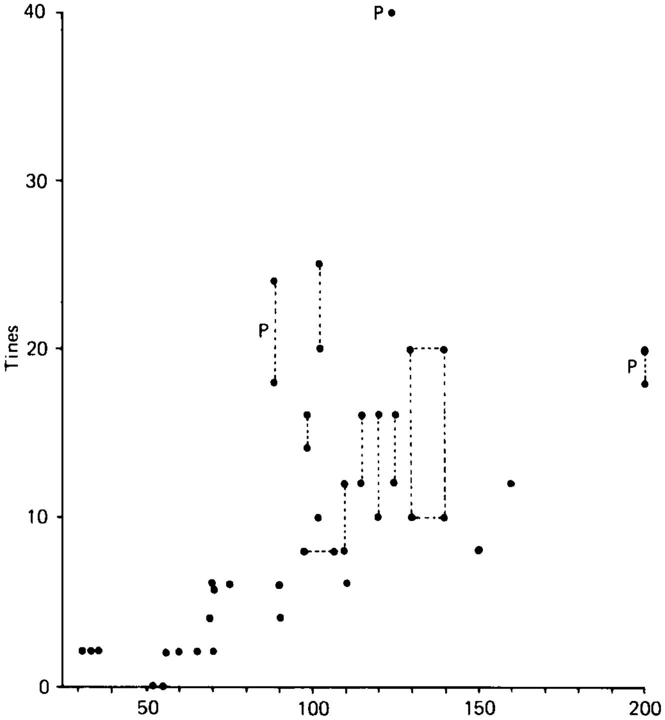

Fig. 10. Relationship, in 30 species of Cervidae, between the number of points (tines) on a full, adult set of antlers and shoulder height of males. Species with palmate antlers are marked P. Ranges of values within a species are joined by broken lines.

such as ruffs, manes, fringes and dark hair, which emphasize the neck and shoulders in males. These may develop for part of the year only. Adornments to a thickened neck are, however, not developed in several otherwise very dimorphic species, such as fallow and sika deer. No deer that I know develops the completely contrasting dimorphic colouration of a bovid such as black buck or sable antelope.

Size dimorphism is poorly documented because of a scarcity of data on females' heights or weights. However, the sexes appear to be of similar sizes in the smallest species, but females are smaller than males by varying amounts in medium and large species. In wapiti and mule deer, females may be half the weight of adult males, in red deer two-thirds, and in caribou and moose about three-quarters of male weight. As in bovids, the largest cervids do not, therefore, show the greatest dimorphism in weight nor the most outstanding weapons. Caribou or reindeer is the only extant cervid genus in which both sexes carry antlers, reminiscent of the arming of both sexes in many large, social, open-country bovids.

Deer seem to display the three forms of growth described for bovids, the first probably occurring in Chinese water deer, tufted deer, musk deer, muntjac species, and perhaps pudus and brocket deer. Determinate bimaturism is well exemplified by red deer (Fig. 13), and probably characterizes many species in the genera *Cervus*, *Axis* and *Dama*. Caribou males grow for 3 years more than females, before growth in jaw length becomes

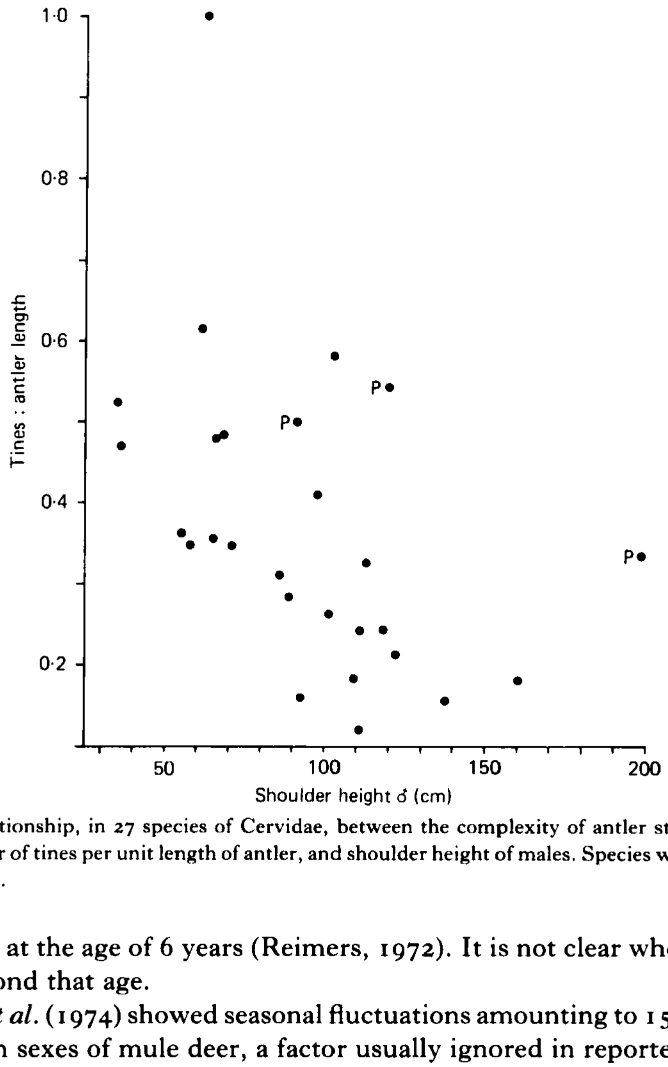

Fig. 11. Relationship, in 27 species of Cervidae, between the complexity of antler structure, expressed as the number of tines per unit length of antler, and shoulder height of males. Species with palmate antlers are marked P.

imperceptible at the age of 6 years (Reimers, 1972). It is not clear whether male weight increases beyond that age.

Anderson *et al.* (1974) showed seasonal fluctuations amounting to 15 % of annual peak weight in both sexes of mule deer, a factor usually ignored in reported species-specific and age-specific weights. Allowing for these fluctuations, they concluded that "male deer...continue to gain weight throughout life, whereas females achieved a constant weight at about 8 years of age". Texan white-tailed deer females stop growing at about 4 years, while male growth may be persistent (Teer *et al.*, 1965).

(3) *Dimorphism and growth in Macropodidae*

There are approximately 45 extant species of kangaroos, wallabies and rat-kangaroos, ranging from 1 to 90 kg in weight. The sexes of bettongs, potoroos and rat-kangaroos in the Potoroinae, between 1 and 3 kilograms in weight, are closely similar in size, colouring, growth and weaponry. These species retain canines (which are not present in most larger macropodids) which, although they do not project beyond the lip, are slightly longer in males than females. The smallest species of Macropodinae, such as banded hare-wallaby, spectacled hare-wallaby, and *Peradorcas concinna*, are also monomorphic (or homomorphic; see below). However, in all larger macropodines,

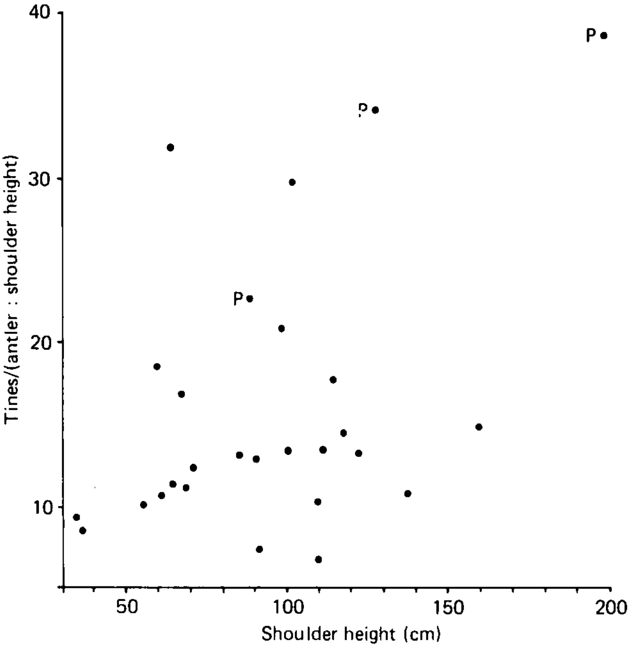

Fig. 12. Relationship, in 27 species of Cervidae, between the relative complexity of antler structure, expressed as the number of tines divided by antler-length (as a proportion of shoulder height), and shoulder height of males. Species with palmate antlers are marked P.

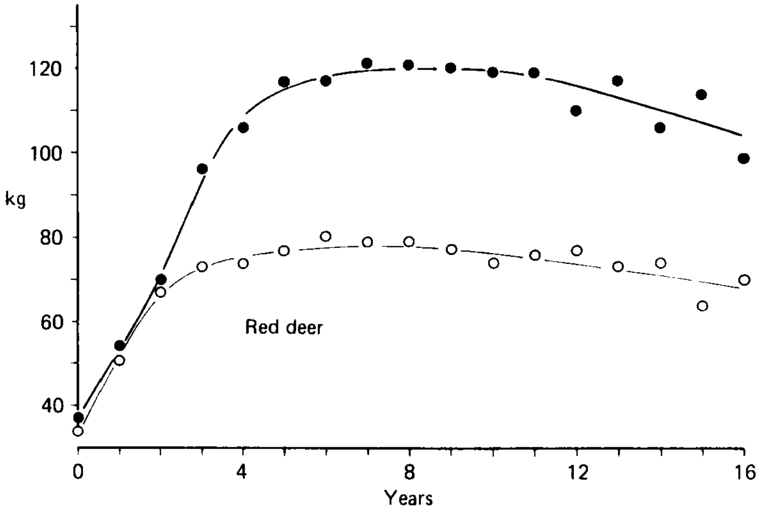

Fig. 13. Growth curves for red deer. The upper curve (black spots) shows values for males, the lower (open circles) for females. Data from Mitchell *et al.* (1977), transformed from eviscerated carcase weights. Curves fitted by eye.

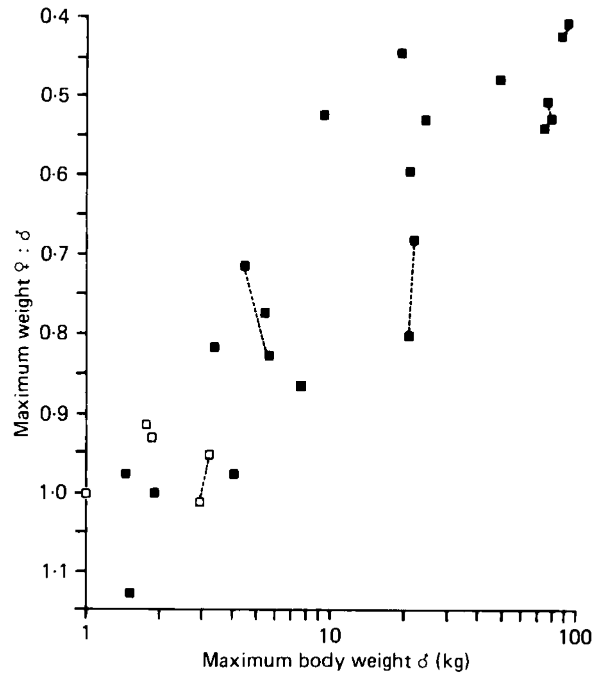

Fig. 14. Relationship, in 21 species of Macropodidae, between dimorphism in maximum adult weights and maximum weight of males. Black squares represent species of Macropodinae, open squares, Potoroinae. Ranges of values within a species are joined by broken lines.

males can potentially grow larger than females, this ability increasing with species' size. The trend for males to be larger than females reaches its peak in the largest extant species, the red kangaroo. In the middle of the range of species' sizes there is a mixture of extremely and only moderately dimorphic species (Fig. 14).

The sexes of two of the largest and most extremely dimorphic species, red kangaroo and wallaroo, differ in colour; in all other species the sexes are similar in colour and markings. However, males in all the medium and large dimorphic species develop heavier arms and shoulders, with larger forepaws and claws, than do females, and the sex of an adult is recognizable from its body shape. Since forelimbs are important in fighting, this is equivalent to developing larger and more conspicuous weapons. Forelimb development is displayed in inter-male aggressive interactions. Forelimb shape varies between macropodid species, although not as obviously as interspecific variation in weapons of bovids and cervids. Males of dimorphic genera of macropodids also develop dermal shields (my unpublished data) analogous to those of antelope, deer and rupicaprids (Geist, 1967; Jarman, 1972, and unpublished data).

One reflection of weapon-size in macropodids is the length of the forearm (elbow to wrist) relative to the length of pes (hind foot) (Jarman & Johnson, in prep.). This value is similar for males and females in the smallest species, but 30–45 % greater in males than in females of the largest species. It bears a significant relationship to the degree of dimorphism in weight (Fig. 15), comparable to the relationship found in bovids (Fig. 6).

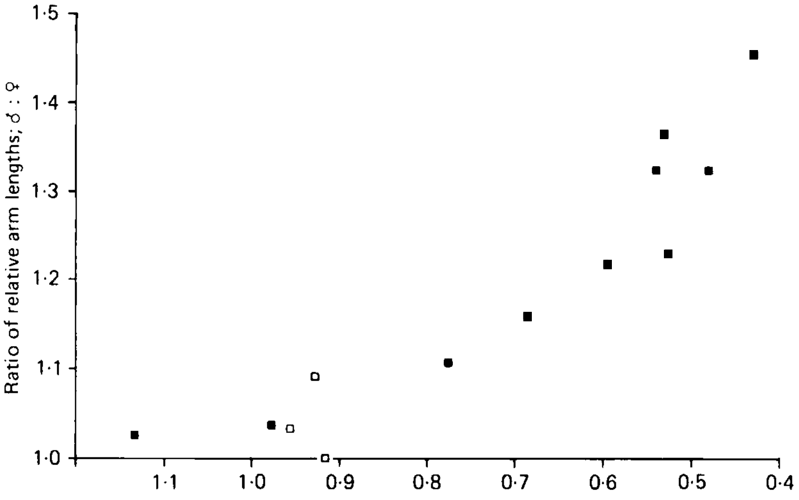

Fig. 15. Relationship, in 13 species of Macropodidae, between dimorphism in relative length of forearm (relative to pes) and dimorphism in maximum adult weight. Black squares represent species of Macropodinae, open squares, Potoroinae.

Macropodids exhibit two of the forms of growth to maturity. The sexes of the smallest species grow at the same rate to similar adult weights which are then maintained (Tyndale-Biscoe, 1968, for boodie; my own data for rufous rat-kangaroo): females, and sometimes males, may start reproducing at just below maximal weight. In medium and large species growth is apparently potentially persistent in males, and in females of some species but at a slower rate, producing dimorphism in maximum adult weight. Both sexes can breed well before reaching maximum weight in these dimorphic species. Female maximum weight in many species is about twice the weight at puberty. In some species female maximum weight is greater than male weight at known physiological sexual maturity. At puberty a female may be one-third (swamp wallaby) to one-fifth (red kangaroo) of the weight of the largest males in the population, a disparity exceeding anything recorded in bovids or cervids (Fig. 16).

Macropodids show relationships between body-size, dimorphism in weight, and weapon-size which are similar to those among bovids and cervids of similar sizes, except that no macropodid over 5 kg adult male maximum weight fails to show a degree of dimorphism in weight. The range of sizes of extant macropodids stops short of the sizes at which large bovids and cervids appear to reduce their degree of dimorphism. It will be interesting to see whether such a reduction characterized some of the recently extinct macropodids which were much larger than red kangaroos.

(4) *Dimorphism and growth in other large, terrestrial, mammalian herbivores*

Difference between the sexes in size and appearance is surprisingly poorly documented for many groups of herbivores. Records suggest that adult males and females reach similar weights, colouring and shapes in black, Indian and perhaps other rhinoceroses; in Malaysian, and perhaps other, tapirs; in Burchell's zebra and perhaps all equids; in collared peccary and perhaps all tayassuids; and in hippopotamus. In extant Tragulidae,

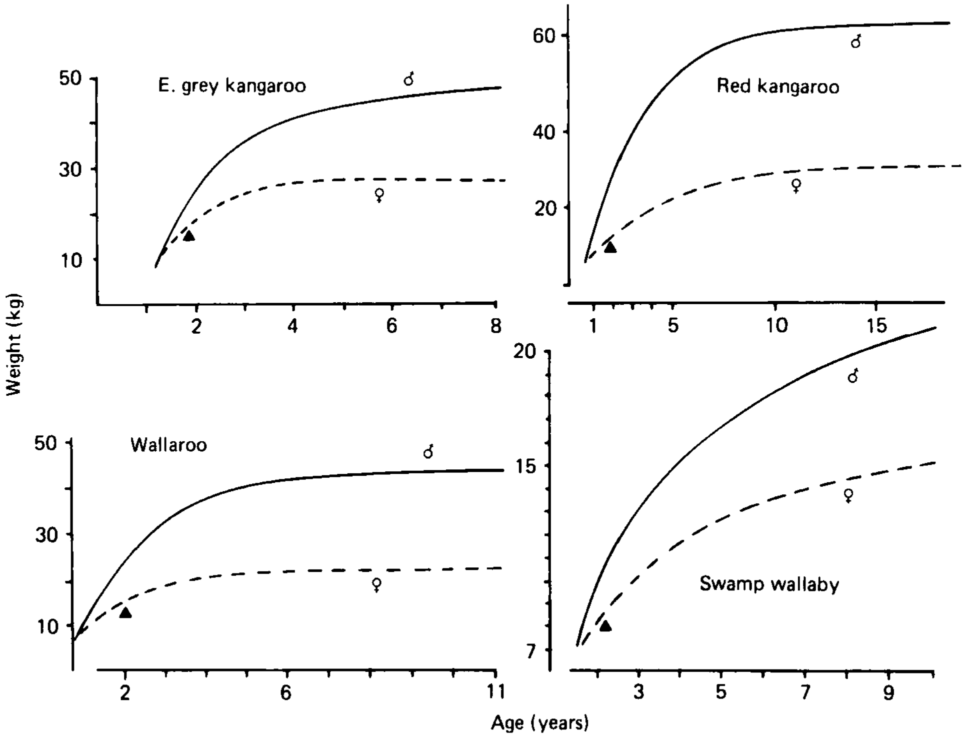

Fig. 16. Growth curves for male and female eastern grey kangaroo, red kangaroo, wallaroo, and swamp wallaby. Data from Frith & Calaby (1969), Harrington (1976), and my unpublished data. Black triangles mark the size at which females may first breed.

females are slightly larger in size (K. Ralls, pers. comm.) but the sexes are alike in colouring and the possession of canines, which are slightly larger in males. These species closely resemble the smallest bovids. Males are slightly larger than females, but similar to them in appearance, in vicuna, camels and white rhinoceros. Males are larger bodied and better armed than females in warthog, wild boar, giant forest hog, and perhaps barbirusa, in the Suidae; in pronghorn, the only extant species of Antilocapridae; in giraffes; and in Indian and African elephants.

The three forms of growth occur amongst these families. The first form (unimaturism) probably occurs in the tragulids, and may also characterize some species of Procaviidae, Tapiridae, Rhinocerotidae, Equidae, Hippopotamidae and Tayassuidae. Determinate bimaturism is found in pronghorn, and perhaps vicuna and camels. Indeterminate bimaturism is well exemplified by African elephant (Fig. 17), and is perhaps found in Indian elephant and giraffe.

These other families display no form of growth or dimorphism which is not found in the bovids, cervids and macropodids, although they do show that there is no overall constancy in the relationships between species' size and dimorphism among mammals.

IV. THE FORMS OF DIMORPHISM: NOMENCLATURE AND DEFINITION

This review of the differences between males and females in growth, size, appearance, and weaponry, makes it clear that values of some of these attributes tend to be associated.

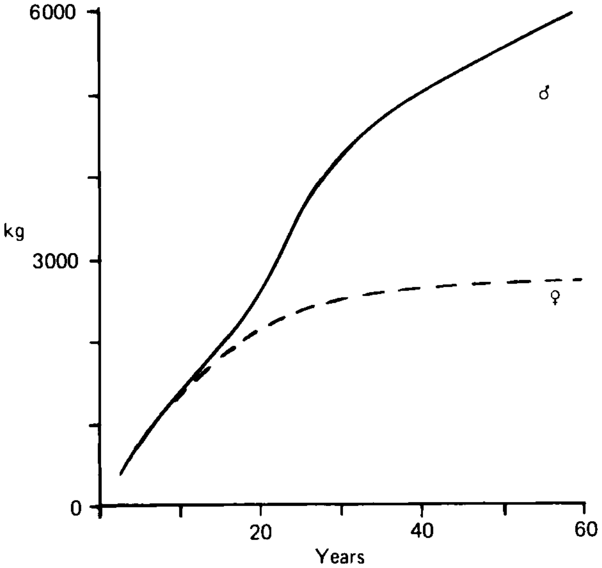

Fig. 17. Growth curves for male and female African elephants. Data from Laws *et al* (1975). Curves fitted by eye.

Earlier classification of species as monomorphic or dimorphic misses some interesting relationships. What follows is an attempt to establish descriptive categories of dimorphism. In the next section, I will suggest that these are also functional categories, having adaptive values in relation to particular features of mating systems.

There is an obvious category of mainly small species in which males and females mature at the same rate, to similar determinate weights, and are almost identical in appearance. Weapons are generally unobtrusive; many carry canines either as their sole weapons or in addition to small horns or antlers. Horns or antlers are sometimes partly hidden by a tuft of hair, while the female dik-dik's erectile tuft may disguise her lack of horns. These species, which include the chevrotains (Tragulidae), duikers, dik-diks and neotragines among the Bovidae, and muntjacs, pudus, musk, brocket, tufted and Chinese water deer among the Cervidae, show HOMOMORPHISM (the sexes being the same shape, size and colouring). There may be a further division between species with armed and unarmed females, but I am uncertain how to treat species whose sexes differ only in the size of their canines.

These homomorphic species contrast with those in which the sexes look different, and mature at different rates to different maximal adult weights, which are maintained for some years. In females of such species weapons are either lacking or much smaller than those of males. Specific male weights range from 30 to 200 kg, or more in a few species. Many of the species whose sexes become conspicuously different in colouring are in this category. These species show DETERMINATE HETEROMORPHISM, there being quite different endpoints to male and female maturation. This category can be further subdivided into: (*a*), those species whose males mature quite early in life (say 1 to 3 years after females) and whose weapons and adornments distinguish sub-adult from adult males, but make no simple distinction among mature adults (these species show

TELIC HETEROMORPHISM) and (*b*), those species whose males reach a maximal weight, several (3 or more) years after females, and whose weapons thereafter continue to change shape, indicating age classes within the pool of mature adults (these species show ECDOCHIC HETEROMORPHISM).

In telic heteromorphic species, change in shape and growth of weapons virtually stops at a well-defined point of maturity. Up to that point there may have been intricate twists and turns in horn growth, permitting fine judgement of sub-adult age (as in impala, lechwe, or blackbuck), or growth along fairly simple curves (as in waterbuck). Examples are illustrated in Spinage (1967, 1971, 1976) and Simpson (1971).

In species showing ecdochic heteromorphism, such as greater kudu (Simpson, 1972), nyala (Rowe-Rowe & Mentis, 1972), bighorn sheep (Geist, 1971) and markhor (Schaller, 1977), horns are still growing and changing shape after the males have entered the breeding pool. Antlers of deer such as red deer increase the number of tines annually until well into the male's maturity. Female horns, if present, do not show the same prolonged growth and changes in shape.

Several large antelopes, including most Alcelaphinae and oryx species, show limited (5–25 %) difference in weight between the sexes, which are coloured and adorned alike. Horns are similar in shape and size in the sexes, although sometimes stouter in males. Examples of their similarities are shown by Mitchell (1965), Huntley (1973), and Talbot & Talbot (1963). These species exhibit HOMOEOMORPHISM, the sexes being similar, but not the same, in appearance.

Different from all these species are those showing HOLOBIOTIC HETEROMORPHISM, so called because males, and sometimes females, continue to grow in body size throughout life, the sexes growing at different rates. This is widespread among the medium and large macropodids and the largest bovids, characterizes African elephants and may be true of white-tailed and mule deer. Persistent growth produces males very much larger than the average breeding female. The male, as he ages, may also gain structures (e.g. a mane) emphasizing his shape and size, although weapons need not be particularly obtrusive. Females are well armed in several of these species.

These categories of dimorphism are not necessarily discrete. It is particularly difficult to distinguish species showing holobiotic heteromorphism from ecdochic heteromorphic species in which maturity in size is long delayed, horn growth is even more extended, and samples of old animals are few. The difference between determinate and indeterminate male growth seems almost academic when male weight-for-age varies individually over a range many times greater than the expected annual growth increment. Growth in many larger bovids, cervids, and macropodids appears to be much influenced by varying environmental conditions, casting doubts on any adaptive arguments based on fine interspecific differences in growth curves. Despite these objections, I believe there are real differences, form of growth being only one of them, within the phenomenon hitherto treated as 'dimorphism', and that these differences have explicable adaptive roots.

Definitions of the categories of dimorphism are summarized in Table 1.

V. DIMORPHISM AND MATING STRATEGIES

This review of physical differences between the sexes indicated that at least one long-cherished simplicity about dimorphism (Huxley, 1932) can be discarded: di-

Table 1. *Definitions of categories of dimorphism used in this paper*

(A) HOMOMORPHIC species: the sexes grow at the same rate to the same adult weights, shapes and colours; weapons may differ but are small and often are hidden. (Strictly these are Determinate homomorphic species; Indeterminate homomorphic species would show persistent growth, identical in the sexes; none is discussed in this paper.)

(B) HETEROMORPHIC species: the sexes differ as adults.
  (i) DETERMINATE HETEROMORPHY: both sexes grow to, and stay at, a maximal weight.
    (*a*) HOMOEOMORPHIC species: the sexes as adults look very similar in shape and colour, and may have similar (often prominent) weapons, but males are slightly (5–20%) heavier.
    (*b*) TELIC HETEROMORPHIC species: males are much larger, and reach adult weight later, than females; they are distinct from females and sub-adult males in shape, weapons, and sometimes colouring; there are no age-class distinctions amongst adult males.
    (*c*) ECDOCHIC HETEROMORPHIC species: as for telic heteromorphic species, except that weapons continue to change after bodily maturity, providing signals of relative age amongst mature males.
  (ii) INDETERMINATE HETEROMORPHY: growth differs between the sexes and is persistent in at least one.
    (*a*) HOLOBIOTIC HETEROMORPHIC species: growth differs in rate between the sexes and is persistent in one or both until death or senility.

morphism is not just an allometric consequence of size. Weapon-size is not related monotonically to specific body-size, nor are differences between the sexes in weight, colouring, shape, or the possession of weapons. However, several facets of dimorphism relate to each other, producing the clusters of characteristics that were used above to discriminate the forms of dimorphism.

Extending the arguments of Darwin (1871), Lack (1968), Selander (1972), Wiley (1974), Emlen & Oring (1977) and Ralls (1977), these clusters of characteristics most probably arose through the different ways in which males typically seek to monopolize mating opportunities. I have argued before (Jarman, 1974, pp. 258–60) that the male mating strategy in antelopes is adapted to the dispersion, grouping, and predictability of occurrence of females. The following discussion assumes that that argument applies generally to the larger, terrestrial, mammalian herbivores, and looks for explanations, in the mating systems, of details of specific dimorphisms.

(1) *Mating systems and homomorphism*

The great majority of homomorphic species are small, cryptic inhabitants of relatively dense vegetation, living singly or in pairs; a minority are large, and solitary (like black rhinoceros or tapir), or social (like hippopotamus, collared peccary, and Burchell's zebra). Spacing in small, homomorphic species frequently involves territoriality, in which both sexes participate (Hendrichs & Hendrichs, 1971; Dunbar & Dunbar, 1974; Dubost, 1971). In such species, which are obligately monogamous (Kleiman, 1977), access to the female for mating is guaranteed by the male's possession of a permanent, resource-sufficient territory. No male in the breeding pool, which consists only of holders of territories, can monopolize matings because of the mutual intolerance of females and the improbability of his being able to hold a double-sized territory. Competition determines which males enter the breeding pool (by gaining territory), but not the relative number of matings thereafter. Reproductive success is probably related to longevity. No advantage would be gained by delayed maturation, or growth beyond that of other males. Nevertheless, it is striking that males are so close to female weight, even slightly below it, in many of these species. Evolution of exact, species-specific male weight must balance the advantages of greater size, in initially gaining territory, against its cost in depriving the female and offspring of the territory's scarce food items. Such a monogamous system, with high male parental investment in defended resources, is theoretically prone to cuckoldry. Perhaps the nearly identical appearance and behaviour of the sexes, even down to 'hidden' weapons, reduces the opportunities for an intruding male to court and mate the female, by increasing the risks inherent in mistakes. The male accompanies the female closely in species such as dik-dik, klipspringer, steenbok and oribi, which live in relatively open habitats.

Homomorphism could be similarly explained in large, monogamous species. Its adaptiveness in the highly polygynous Burchell's zebra is at first puzzling; homoeomorphism, as in the alcelaphines that are so ecologically similar to zebras, might seem more appropriate. But, unlike the alcelaphines, zebra males invest in offspring through defence of their group of mares and foals against predators. Perhaps the anti-cuckoldry argument used above can be extended to zebra; an intruding male would risk being caught *flagrante delicto* if he cannot distinguish the consorting male from his females.

The rufous rat-kangaroo, a small, non-territorial, homomorphic species, spends its day in a nest, emerging at night to dig for roots, tubers and underground fungi which it seeks in a large home-range overlapping the ranges of a few other individuals of both sexes. I argue the adaptiveness of monomorphism in the species thus. A male monitors the location and reproductive status of females in his home-range, nightly if possible, paying particular attention to a female for some nights before oestrus. He cannot nest, nor continuously feed, with the female, so cannot constantly defend access to her, although he will be aggressive towards other males when he is consorting with an oestrous female. Density of these cryptic animals and visibility in their habitats are so low, and relative home-range size so large, that the probability of encountering females in oestrus by chance is negligible. A male invests in knowledge of the status and locations of females to gain matings. Greater ranging ability, gained from greater size, might reduce the male's efficiency of monitoring any one female, intensity of coverage, rather than extent of range being the key to knowledge. Although greater, but therefore deferred, mature size might benefit males in fighting, the opportunity to monopolize females through inter-male aggression is very limited; rapid maturation might be more valuable. A female can easily fight off males that court too eagerly or untimely. While a male needs to be of similar size to a female so as not to be cowed by her, a female may need to match male size to defend access (for herself and her offspring) to nest-site refuges and food items. The rufous rat-kangaroo's homomorphism arises from the balance between those adaptive pressures.

(2) *Mating systems and telic heteromorphism*

This section's introductory assumption (p. 20), that male mating strategy is adapted to the dispersion, grouping and predictability of occurrence of females, must be particularly remembered in considering mating systems and the remaining styles of heteromorphism. A male cannot limit the direction or distance of movement of females in a group against their inclination. Such control would have to be imposed by the threat to a female of some detriment greater than that of staying in the area that she wants to leave. With minor exceptions, physical injury by the male would be the only feasible threat, but it would need to be more than a bluff to be effective. A male could attack only one female at a time, losing the rest of the group. A male's ability to court oestrous females that have learned to avoid his attacks would be diminished. His time spent attacking females to control their movements would diminish his ability to keep other males from them. Eventually the strategy of control through attack would be maladaptive since it would produce females that were injured, or resource-depleted, or both. In a population containing both controlling and non-controlling males, females would probably mate preferentially with the latter through avoidance of the former. Thus, in species whose food requirements and forms of avoidance of predation make grouping adaptive for females, the male's strategy should comply with the female's grouping and ranging tendencies.

Female populations in telic heteromorphs are at least temporarily sedentary. They form open-membership groups whose size responds dynamically and optimally to several environmental factors, availability and dispersion of food items being particularly important (see Jarman & Jarman, 1979, for examples). Males typically attempt polygamy by gaining territories, established regardless of the immediate presence of females and held for an appreciable time. Territory-holders emerge as currently the most dominant individuals in a bachelor hierarchy, to which they may (impala: Jarman, M. V., 1979), or may not (waterbuck: Spinage, 1969), return on losing territorial status. Once gained, the territory allows the male to attach his dominance to a spatially fixed, demarcated and defended area, within which he is dominant over all other males, and where he alone can court and mate with females. Females can move between territories in their open-membership groups; their use of habitats often varies seasonally. Females are not attracted by individual males, but rather by the resources a territory holds. Profitable territories are those most predictably attracting oestrous females. Reproductively successful males are those holding territories that are large (pronghorn: Kitchen, 1974), or resource-rich, or both (impala: Jarman, M. V., 1979), especially during seasonal peaks in frequency of oestrus.

This mating system discriminates among all males to produce the dominant holders of territories, and sometimes again from within that group to differentiate between holders of highly profitable and less profitable territories. Thus competition among males for mating rights is severe. Contenders for territory have reached the top of a hierarchy that is age-based among sub-adults, but determined by individual prowess thereafter. Sub-adult stages are clearly signalled by horn shapes. Dominance, especially of territory-holders, is displayed in postures, appearance, smell and behaviour, and must be supported by fighting ability. Serious fighting, when it occurs, can be crippling or lethal. It is vital that a male competing for territory has developed the weight of body, neck musculature, horn size and dermal shield that signify maturity.

Territorial males show varying tolerance of bachelors, but usually drive them out of female groups. There, and in the hierarchical tensions of bachelor herds, young males may benefit by clearly signalling (via horn-shape, and colour) their sub-adult status. Similarly they must behave subordinately and not court females if they wish to survive.

Two obvious questions are: why not attempt polygamy by other strategies; and why does growth of body and weapons in males cease? An area large enough to cover the home-ranges of several females, which might possibly then be herded permanently within it, is undefendable. The non-territorial strategy of ranging with a monopolized group of females is opposed by the fragility of those groups and risks of incursion by other males, and would limit the male's contact to the group's changing members. The evolved territorial strategy reduces the risk of incursions, expands his contact to all females that pass through his territory, and offers better than average contact with oestrous females if he can hold the right territory at the right time, female choice of habitat and seasonality of oestrus being reasonably predictable.

The size of territory that a male can efficiently control is limited partly by factors such as visibility, rather than by fighting ability alone. Beyond a point no extra area is gained by being bigger, or better armed, than rivals. Holding territory costs time and attention, and depletes successful males rapidly (Jarman, M. V., 1979); this may limit the handicap that a male can carry in the way of horns. Because females are fairly evenly dispersed, in groups, there is a limit to the proportion of the population that a male can hope to monopolize. As a general rule, if there are N equal units of females that could be monopolized in the population, a male will gain nothing by being well armed or big enough to rise above the Nth rank. Indeed, he could only lose by paying in time and energy to grow larger in body or weapons.

(3) *Mating systems and ecdochic heteromorphism*

Males of species such as red deer and big-horn sheep attempt polygyny, but without using spatially stable territories to localize their dominance, and without permanently accompanying a group of females. Females roam in open-membership groups, as do males for most of the year. Red deer and sheep mate during a sharply defined rut, before and during which males compete to establish personal dominance in the local hierarchy, using that dominance to keep rivals away from temporary groups of females. Dominance is frequently re-asserted physically and advertised by calls, smell and postures (Geist, 1971; Clutton Brock *et al.*, 1979). However, less dominant males, lurking near the defended female group, await the opportunity for quick mating undetected by the more dominant male ('kleptogamists').

Dominant males in this system lack the security of undisturbed mating afforded by a territory, but have the opportunity to pursue females actively rather than gaining them passively through the attractions of a good territory. Where females are concentrated, in open country and synchronously oestrous, one or a few males would be unable to defend territories containing all the females against all the other males invading simultaneously. Territories might also be unprofitable when species, such as greater kudu and nyala, live in relatively dense habitat, and females roam in small groups over large ranges.

As for telic heteromorphs, intense intrasexual competition accounts for dimorphism in body size and weaponry, but leaves open the questions: Why not continue to grow in weight, and why continue to increase size of weapons? There may be a physiological limit to the body size males can sustain; all these species live in seasonal environments and their weights fluctuate seasonally. However, it is likely that, as for telic heteromorphic species, growth in size ends because the proportion of the females that a male can guard is eventually limited by factors outside his control, in this case the size of group that females will tolerate. Not even a super-male could gather and keep all the females in one group, so growth beyond the normal maximum body size for that population would be profitless. However, since courtship and mating must be carried out in full view of potential kleptogamists and rivals, the signal function of weapons, and an emphatically 'male' appearance, are important. Geist (1966, 1971) has discussed antlers and horns as indicators of rank for both sub-adults and adults within the breeding pool.

(4) *Mating systems and homoeomorphism*

Alcelaphine antelopes, for their size, show surprisingly little sexual dimorphism in size, colouring, adornment and weapons. All species live in open country, moving in open-membership groups, sometimes in vast aggregations; populations might be either migratory, nomadic, or sedentary, some occasionally having to change from one mode to another. Most populations mate in a sharply defined rut. Males in sedentary populations behave like telic heteromorphic species, graduating from dominance in a bachelor hierarchy to holding spatially defined territories which afford them exclusive mating rights with females that pass through. In nomadic or migratory populations, males do not hold fixed territories but move with the females, using their dominance to keep other males away from a patch of ground and the females it temporarily contains (Estes, 1969; David, 1973; Gosling, 1974; von Richter, 1971).

Because these species can occur at very high densities in open country, no one male can monopolize access to a high proportion of the oestrous females. Increase in size of territory would worsen the already high rate of interruption of mating by intruding males. This partly explains the lack of great dimorphism in body size, but leaves open the question of why the sexes are so alike in weapons, shape and colouring. Females might need horns to defend their precocial young against open-country predators. The effectiveness of such defence by female wildebeest against single hyaenas (Kruuk, 1972) and female hartebeest against jackal and cheetah (my observations) has been noted; K. Ralls (pers. comm.) has similarly noted the ferocity of attack by captive female oryx against a predator. Estes (1974) states that a hierarchy exists at times among wildebeest females; whether it is typical of homoeomorphic females is not known and its function is obscure.

Lack of clear, long-range distinction between the sexes characterizes many open-country larger herbivores besides the alcelaphines, such as zebras and oryx. For all these species it could reduce a predator's ability to fix on a target. However, in nomadic alcelaphines, and oryx, females and males live in the same aggregations, or at least in visual proximity, for much of the year. It may be that females need weapons to repel the courtship of young, unproven males.

(5) *Mating systems and holobiotic heteromorphism*

Holobiotic heteromorphic species have a male mating strategy that relies upon a male exerting his dominance over rivals in the presence of an oestrous female, without that dominance being attached to any area.

African buffalo live in large, closed-membership herds of both sexes (Grimsdell, 1969; Sinclair, 1977). Males maintain a hierarchy, in which rank is related to body size and most matings are gained by the higher ranking individuals. Oestrus is not closely synchronous throughout the herd. Sinclair (1977, p. 102) describes how increasingly more dominant bulls succeed each other in following an oestrous female, the last staying and mating with her through the few days of oestrus: "The rapidity with which the dominant animals took over the female indicated their efficiency in securing the females in estrus...Proestrus lasts as long as 2 days...so the top bulls in the social hierarchy have ample time to secure the females simply by watching the other males".

The American bison is a holobiotic heteromorphic species which mates in a brief rut, during which females and juveniles congregate. Adult males join these groups, seek out oestrous females and tend them, attempting to keep other males away. Dominance, determined by fights both in the presence of and away from oestrous females, allows a male to supplant a subordinate that is tending a female (Lott, 1974). The mating system in the European bison is probably similar. Tulloch (1979) describes water buffalo males as fighting most when cows were in oestrus. A male tends an oestrous female, driving off other males if he is sufficiently dominant. Males appear to succeed each other in tending successive oestrous females in a group. Schaller (1967) records a hierarchy in gaur, based on size. Large, black, gaur males wander extensively during the rut, checking female herds. They tend oestrous females in much the same manner as buffalo or bison males.

Giraffe females live in loose, open-membership groups. Males, which as adults have enormous home-ranges, wander alone between groups, monitoring females for signs of oestrus. An oestrous female is escorted, perhaps for days. A larger male may usurp an oestrous female from a smaller, escorting male, an absolute hierarchy being evident in her presence (Leuthold, 1979). Serious fighting between males can occur in the presence of an oestrous female (C. Mejia, cited by Moss, 1975); but a hierarchy among the males of a district is established by sparring, not in the presence of oestrous females.

Female and juvenile African and Indian elephants live in closed-membership groups of matrilineal relatives (Douglas-Hamilton, 1972; Kurt, 1974; Olivier, 1978). Males are found solitarily or in open-membership groups (Hendrichs & Hendrichs, 1971; Croze, 1974), not usually accompanying females. However, in both species, males intermittently come into 'musth', a state signalled by secretion from a temporal gland. African elephant males in musth range widely, feed little, and frequently visit female herds (C. Moss, pers. comm.). Of Indian elephants Kurt (1974, p. 630) reports: "Males in musth seem to control waterholes, frequently urinating and defaecating, more than males not in musth". They are also more attentive to females and aggressive towards other males. In the Indian elephant population studied by Kurt and the African one studied by Moss, males came into musth sequentially, so that only one or two were in musth simultaneously. If two coincide in musth and join the same herd, the stronger male drives out the weaker, which may then drop out of musth (Kurt, 1974). Musth might last 1–5 weeks.

Mule deer males increase in size throughout life (Anderson *et al.*, 1974; Roseberry & Klimstra, 1975), although female growth terminates; white-tailed deer may do the same (Teer *et al.*, 1975). Dominant males are reported to wander widely in the rut, seeking oestrous females, which they will tend for several days.

Mating is monopolized by the most dominant male that detects an oestrous female in both group-living and solitary kangaroos, wallabies, pademelons and swamp wallabies. An oestrous female of social species, such as red and eastern grey kangaroos, may be pursued by several males in descending order of size, pursuit by small males attracting the attention of larger ones. Larger males of red kangaroo, eastern grey kangaroo, wallaroo (Osazuwa, 1978) and whiptail wallaby (Kaufman, 1974) move widely, checking females for signs of oestrus; in some species a male may associate for some days with a female before and during oestrus. Fighting between equal-sized males can occur both near and away from oestrous females. Male dominance in medium and larger macropodids usually relates to size. Large male red kangaroos are more likely than smaller males to be found in the habitats favoured by females (C. N. Johnson, 1979). In swamp wallaby and red-necked pademelon, large males are found near resources that females will preferentially use (K. A. Johnson, 1977, and my own observations).

In these examples of species showing holobiotic heteromorphism, male dominance is related to size and can be asserted, by fighting if necessary, in the presence of an oestrous female. Dominant males seek females in, or approaching, oestrus; evidence of oestrus may be more prolonged than in other herbivores, females being tended by a male or males for 2 to 5 days before and during full oestrus. The male's strategy emphasizes wide searching for oestrous females, as well as tactics such as watching other males and frequenting habitats or resources used by females; guarding a female throughout oestrus; and the ability to assert dominance in the presence of an oestrous female, as well as prior establishment of dominance.

The instantaneous dominance, on which success in this strategy depends, rests upon fighting ability, which depends on body size. The bigger a male becomes, the more males in the population he can dominate. Assuming a maximal growth rate, greater size can be achieved only by prolonging growth, which requires prolonged survival. These species should evince strong selection for aspects of survivorship, and illustrate a socioecological truism; it is not necessary for all individuals practising a strategy to be successful (many males will die before being old or large enough to gain mates); it is necessary only that the successful individuals should be practising that strategy.

While size is important in fighting, weapons of holobiotic heteromorphs are generally unimpressive for the size of the species. Females carry weapons at least half as large as the males', except in *Odocoileus* deer, and some elephant populations. Female elephants and bison have been seen using their weapons to ward off males; a macropodid female may cuff males, especially young males, trying to inspect her pouch or cloaca, a preliminary to courtship. These species' societies are spatially relatively unorganized, and females may potentially be contacted by males of all ages. Her weapons may be part of the female's evolved defence against being mated by young males whose survivorship is unproven. Since survival is the arbiter of male reproductive success, a female mating with a young male is risking her offspring's inheritance.

Oestrous females in these species are dispersed in such a fashion that a greater proportion of them could potentially be monopolized by a dominant male practising this free-ranging strategy than by one trying to hold a group of females or a territory. Moreover, there is no obvious limit to the proportion that could be monopolized. Under the circumstances it is appropriate that males should grow throughout life. However, since young males may occasionally mate if older males are absent or occupied, there may be tactical variation in the form of the growth curve.

VI. MATING SYSTEMS, DIMORPHISM, AND OTHER ASPECTS OF SOCIOBIOLOGY

These reviewed forms of mating system and dimorphism relate to the probable distributions of reproduction through the life histories of males. A young male of a small, territorial, homomorphic, monogamous species such as dik-dik, once he gained territory, could hope to hold it and to reproduce for the rest of his life. Selection should favour early maturity and acquisition of territory. An impala male (polygamous, with telic heteromorphism) might have to wait until the age of 3 or 4 years before gaining territory, and would have the best chance of holding prime territories only until he was 6 to 8 years old. Big-horn sheep or red deer (polygamous, with ecdochic heteromorphism) are probably reproductively most successful between 5 and 10 years old, success declining thereafter as they retreat to the tails of the rut. Homoeomorphic wildebeest may have a similar delay before some years of reproductive success. Chances of successful reproduction for male holobiotic heteromorphs improve with age until death or a brief decline preceding it.

Thus there is a trend in average age of male parent in these forms of mating system and related dimorphism. Because of the correlations of body size and age at puberty, and body size and mating system, there is also a weak trend in average age of mother. However, there should be a stronger trend in average difference between parents' ages with mating system, this being least in monogamous, homomorphic species, and greatest in polygamous, holobiotic, heteromorphic species. With widening disparity in parental age, females should increasingly recognize and choose appropriately aged males, while males signal attainment of that age; and young males should strive to survive rather than to emulate older males. This last characteristic is hard to quantify, but young males should invest less than do prime-age males in courtship and more in avoiding injury and death. They may live in the security of a herd, rather than solitarily, and avoid confrontation with socially dominant prime-age males, either by subordinate behaviour while remaining in the same herd, or by moving well away. The result is an increasing complexity in the individual male's social experience and in the population's social organization.

In small homomorphic, monogamous species, a male lives through few social phases (like females); the population consists of adult holders of territories and their dependent juveniles, with very few, ephemeral, territory-less animals. An impala male, showing telic heteromorphism, grows from juvenile to sub-adult bachelor, prime-age bachelor, territory-holder, and post-prime bachelor; he may change from bachelor to territory-holder several times. Similar complexity characterizes species showing ecdochic heteromorphism and homoeomorphism, while for species showing holobiotic heteromorphism inter-age relationships for a maturing male are ever-changing, but without distinct phases. The male of a holobiotic heteromorphic species must to some extent evaluate the relative rank of each male he encounters, the activities of dominant males doing little to define social contexts in which a male would automatically know the appropriate way to treat any other male. Reactions towards other males by males of homomorphic monogamous species, by contrast, are fully defined by context; a territory-holder can treat any other male, except his dependent son, as an intruder. Reactions for males in other systems fall between these extremes.

A female's selection of an appropriately aged mate can have little effect on her male offspring's reproductive potential in homomorphic species; any male in a position to court a female is as reproductively successful as any other. In all species in which some males can thwart the reproductive hopes of others, she should avoid being mated by a thwartable male. In most territorial, heteromorphic or homoeomorphic species, the matter is settled for her by competent males keeping the inept away from her. However, in species showing ecdochic, and particularly holobiotic, heteromorphism, she may be more exposed to inappropriate mates, and required to act against them herself. Females in many of these species are armed, and males often have evident signals of age or rank. Despite those signals she may demand an investment in courtship time that far exceeds that of species showing telic heteromorphism. A female of a species showing holobiotic heteromorphism can hope that a superior male will arrive at any stage of her prolonged oestrus; a female of a species showing telic heteromorphism can only ensure that the right class of male courts her; a homomorphic, paired female has no new choice to make at oestrus. Courtship or consorting time before copulation falls from several days in holobiotic heteromorphic species to a few hours at most in telic heteromorphs. It may be still briefer in some homomorphic species.

VII. ECOLOGICAL DIFFERENCES BETWEEN CLASSES AND INDIVIDUALS

Among small, monogamous, homomorphic herbivores, males, females, and their dependent young share the same habitats and resources, although they may differ in their activity budgets (Dunbar, 1979). In contrast, adult males and females of many heteromorphic species differ in their use of habitats, daily time of use of resources, and diets. In many eurasian deer and caprines the sexes spend much of the year apart. Even in migratory species (caribou, wildebeest), the sexes may be grouped separately within the moving population.

Sometimes the differentiation appears to result from dominant males keeping other males away from females; in impala all classes mingle freely once territoriality has collapsed (Jarman & Jarman, 1973), suggesting that it was the behaviour of the territorial males that organized the society spatially. Geist & Petocz (1977) suggest that males of pronghorn and 'some old-world cervids' can remain with females after the rut only be shedding their weapons; otherwise predators would too easily recognize them as weakened, post-rut males. Similar reasons, they argue, induce male big-horn sheep, which do not shed their horns, to dissociate from females after the rut. They also suggest that such a separation is adaptive because it leaves more pasture for the rutting males' offspring. There are objections to these arguments. Males of some deer separate from females despite shedding antlers, while post-rut impala males associate with female while retaining horns. The suggested strategy requires the co-operation of all males, whether successful in the rut or not; and it is not carried to its logical conclusion in that young males are not herded away from the females (admittedly at some cost) by the rams. The suggested strategy does not generalize well.

A more general explanation might derive from the need of males of polygamous, heteromorphic species to monitor their individual ranks within the local male population. Uninterrupted mating depends on dominance which is established at considerable physical risk; even in well matched fights, deaths are quite common (see Clutton-Brock *et al.*, 1979). Deaths would be frequent if males did not scrupulously avoid confrontation with clearly superior individuals (as is too easily demonstrated in mismanaged captivity). A male most safely achieves breeding status only by continuous self-assessment relative to other males. The remaining risk when he commits himself to challenge for breeding status will be much less than if he had matured in isolation. Thus heteromorphic males should be in regular evaluative contact when not breeding; breeding males too may benefit by monitoring their own prowess.

Some observations on differential distributions of sex and social classes support this argument. Impala bachelors do not totally abandon the area occupied by territories, and a territorial male without females will join a bachelor herd in his territory, exerting his dominance over each member (Jarman, M. V., 1979). Separation of the sexes in elephants or kangaroos is similarly far from total.

In big-horn sheep and red deer, most males of breeding age join females only during the rut, while young males, and some old males in big-horn sheep (Geist, 1971), remain with females at all times. Under the present conventions, a breeding-age male that stayed with females all year would suddenly at the start of the rut have to fight a succession of strange males, against whom he had had no chance to test his prowess. In red deer and sheep, dominant males leave before the end of the rut, presumably when loss of a few matings in the current year is outweighed by increased probability of survival through the winter to participation in the next rut. The rutting grounds are female wintering grounds in sheep, and males must leave them entirely to avoid the aggression of late-rutting males. Any male that wishes to keep up his self-assessment should leave with the others.

Feeding groups of herbivores sometimes consist of animals of similar age or physiological status, perhaps to maintain individual anonymity under threatened predation, or cohesion through animals seeking food items of similar quality in similar quantities. The latter argument should deter post-rut males from associating with pregnant, or lactating, females, whose nutritional requirements might be very different from the males'. Males of red deer (Mitchell *et al.*, 1976) and big-horn sheep (Geist, 1971) are reported to inherit ranges by following other males. Tradition may stabilize the habit of separation of males from females, once it has been initiated.

There is still too little known about ecological differences between the sexes in these highly heteromorphic species. However, as a final twist to the theme of ecological determination of social systems, it is interesting to contemplate what sorts of species have niches broad enough to support such ecologically divergent social classes.

VIII. SUMMARY

Sexual dimorphism in mammals is not entirely satisfactorily explained by the models that are advanced to account for it among birds. This may be because species-specific styles of being dimorphic, and of attaining mature dimorphic state, are not clearly recognized. Mature dimorphism is a syndrome involving body size, appearance and weaponry; each facet and the whole syndrome may have functions in both fighting and signalling. The mature dimorphic stage has to be reached by growth and change from juvenile and sub-adult states.

The occurrence of the separate facets of the dimorphic syndrome are reviewed in species of Bovidae, Cervidae and Macropodidae, large, diverse families of eutherian (the first two) and metatherian mammals, which have broadly similar ecological adaptations. In each family the smallest species tend to be homomorphic, with small, inconspicuous weapons. Greatest dimorphism in size is found in medium-sized bovids and cervids, and the larger macropodids (in which no species exceeds 100 kg male weight); the range of species showing greatest dimorphism in size also shows the most exaggerated weapons. Mature dimorphism is reached by different patterns of growth, which may be determinate and similar in the sexes (leading to homomorphism), determinate but differing between the sexes, or indeterminate and differing, both of which lead to heteromorphism.

The syndromes of dimorphism and patterns of growth are associated and a classification of styles of dimorphism is presented. The adaptiveness of the styles is suggested in terms of what is known of the socio-ecology, in particular the male reproductive

strategies, of the species. The various styles of heteromorphy appear to be associated with males' way of achieving polygyny: such as by non-resource-based territoriality, by dominance-determined access to oestrous females, or by wandering and formation of a consortship with pro-oestrous females. The relevance of the species' ecology of use of resources to these styles of dimorphism and mate-acquisition is briefly discussed.

IX. ACKNOWLEDGEMENTS

I am grateful to Professor J. H. Bishop for his helpful discussion of terms to describe styles of development of dimorphism; to D. G. Kleiman and C. N. Johnson for commenting on a draft; and particularly to Katherine Ralls and Peter Waser for their detailed and constructive criticisms, suggestions, and provision of references. I also thank Audrey Peters for her cheerful and patient preparation of the typescript.

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XI. APPENDIX 1

Animals mentioned in the text.

Macropodidae	
Rufous rat-kangaroo	*Aepyprymnus rufescens*
Bettongs	*Bettongia* spp.
Boodie	*B. lesueur*
Desert rat-kangaroo	*Caloprymnus campestris*
Potoroos	*Potorous* spp.
Spectacled hare-wallaby	*Lagorchestes conspicillatus*
Banded hare-wallaby	*Lagostrophus fasciatus*
Eastern grey kangaroo	*Macropus giganteus*
Whiptail wallaby	*M. parryi*
Wallaroo or euro	*M. robustus*
Red kangaroo	*M. rufus*
Red-necked pademelon	*Thylogale thetis*
Swamp wallaby	*Wallabia bicolor*
Elephantidae	
Indian elephant	*Elephas maximus*
African elephant	*Loxodonta africana*
Hippopotamidae	
Hippopotamus	*Hippopotamus amphibius*
Suidae	
Babirusa	*Babyrousa babyrussa*
Giant forest hog	*Hylochoerus meinertzhageni*
Warthog	*Phacochoerus aethiopicus*
Wild pig (boar)	*Sus scrofa*
Tayassuidae	
Collared pecarry	*Dicotyles tajacu*
Rhinocerotidae	
White rhinoceros	*Ceratotherium simum*
Black rhinoceros	*Diceros bicornis*
Indian rhinoceros	*Rhinoceros unicornis*
Tapiridae	
Malaysian tapir	*Tapirus indicus*
Equidae	
Burchell's zebra	*Equus burchelli*
Camelidae	
Camels	*Camelus* spp.
Vicuna	*Vicugna vicugna*
Giraffidae	
Giraffe	*Giraffa camelopardalis*

Tragulidae	
Chevrotains, or mouse deer	*Hyemoschus* and *Tragulus* spp.
Bovidae	
Big-horn sheep	*Ovis canadensis*
Thin-horn sheep, Dall sheep	*O. dalli*
Urial and mouflon	*O. orientalis*
Markhor	*Capra falconeri*
Tahr	*Hemitragus* spp.
Saiga	*Saiga tatarica*
Serow	*Capricornis* spp.
Musk-ox	*Ovibos moschatus*
Duikers	*Cephalophus* and *Sylvicapra* spp.
Dik-diks	*Madoqua* spp.
Steenbok	*Raphicerus campestris*
Klipspringer	*Oreotragus oreotragus*
Oribi	*Ourebia ourebi*
Gazelles	*Gazella* spp.
Impala	*Aepyceros melampus*
Waterbuck	*Kobus ellipsiprymnus*
Lechwe	*K. leche*
Wildebeest	*Connochaetes* (or *Gorgon*) spp.
Oryx	*Oryx* spp.
Sable antelope	*Hippotragus niger*
Greater kudu	*Tragelaphus strepsiceros*
Nyala	*T. angasi*
Black buck	*Antilope cervicapra*
Nilgai	*Boselaphus tragocamelus*
American bison	*Bison bison*
European bison	*B. bonasus*
Gaur	*Bos gaurus*
Water buffalo	*Bubalus bubalis*
African buffalo	*Syncerus caffer*
Pronghorn	*Antilocapra americana*
Cervidae	
Chinese water deer	*Hydropotes inermis*
Tibetan muntjac or tufted deer	*Elaphodus cephalophus*
Musk deer	*Moschus* spp.
Muntjac species	*Muntiacus* spp.
Andean deer or huemuls	*Hippocamelus* spp.
Marsh or swamp deer	*Blastoceras* spp.
Pudus	*Pudu* spp.
Brocket deer	*Mazama* spp.
Mule and black-tailed deer	*Odocoileus hemionus*

White-tailed deer	*O. virginianus*
Roe deer	*Capreolus capreolus*
Elk or moose	*Alces alces*
Red deer	*Cervus elaphus*
Wapiti or American elk	*C. canadensis*
Sambar or rusa	*C. unicolor*
Schomburgk deer	*C. schomburgki*
Sika	*C. nippon*
Barasingha	*C. duvauceli*
Chital or hog deer	*Axis* spp.
Fallow deer	*Dama dama*
Caribou or reindeer	*Rangifer* spp.

XII. APPENDIX 2

Sources of information on body weights and dimensions, weapons, colouring and growth of the animals discussed in this paper. My unpublished data are not listed. Anderson *et al.* (1974), Ansell (1965), Bandy *et al.* (1970), Banfield (1974), Blood *et al.* (1970), Bunnell & Olsen (1976), Christie (1964), Clutton-Brock *et al.* (1980), Dorst & Dandelot (1970), Dunnet (1962), Frith & Calaby (1969), Geist (1971), Hanks (1972), Hansen (1965), Harrington (1976), Hitchins (1968), Howells & Hanks (1975), Hughes (1962), Jarman & Johnson (in prep.), Johnson (1973), Johnson (1977), Johnson & Sharman (1976), Kellas (1955), Kitchener & Sanson (1978), Kurt (1974), Laws *et al.* (1975), Ledger *et al.* (1967), McEwan (1968), McEwan & Wood (1966), Maynes (1976), Medway (1969), Mitchell (1965), Mitchell *et al.* (1976, 1977), O'Gara (1970), Pearse (1981), Penzhorn (1974), du Plessis (1972), Quimby & Johnson (1951), Reimers (1972), Robinette & Child (1964), Roseberry & Klimstra (1975), Rowe-Rowe & Mentis (1972), Schaller (1967, 1977), Simpson (1971, 1972), Sinclair (1977), Smuts (1975), Southern (1964), Spinage (1967, 1969, 1971, 1976), Talbot & Talbot (1963), Teer *et al.* (1965), Tyndale-Biscoe (1968), Valdez *et al.* (1977), Walker (1975), Whitehead (1972), Wilson & Child (1964), and Wood *et al.* (1962).